

Larval Life History Responses to Food Deprivation in Three Species of Predatory Lady Beetles (Coleoptera: Coccinellidae)

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ABSTRACT We studied life history responses of larvae of three coccinellid species, *Coleomegilla maculata* (DeGeer), *Hippodamia convergens* Guerin-Meneville, and *Harmonia axyridis* (Pallas), when deprived of food for different periods of time during the fourth stadium. The coccinellid species did not differ in starvation resistance when larvae were starved throughout the stadium; however, for larvae fed only on day 1 of the stadium, *H. convergens* had the highest starvation resistance, followed by *H. axyridis* and then *C. maculata*. Percentage weight loss of larvae was affected by food deprivation period and coccinellid species. Both *C. maculata* and *H. axyridis* lost significantly more weight than *H. convergens* when starved throughout the fourth stadium. When deprived of food for 4 d of the stadium, *C. maculata* lost a higher percentage of initial body weight than *H. axyridis*. Percentage weight loss of *H. convergens* did not differ from that of *C. maculata* or *H. axyridis*. The weight of fourth instars and adults declined in an accelerating pattern as food deprivation period increased. However, food deprivation period had no significant effect on pupal development time for any of the three species or on larval development time for *C. maculata* and *H. convergens*. The increase in *H. axyridis* larval development time as a result of an increase in food deprivation period was curvilinear. Based on this laboratory study, it would seem that *H. convergens* is better able to cope with acute nutritional stress than either *C. maculata* or *H. axyridis*.

KEY WORDS food deprivation, life history traits, *Coleomegilla maculata*, *Hippodamia convergens*, *Harmonia axyridis*

Food scarcity is generally considered to be one of the key factors that shape the structure of insect communities by constraining the growth of populations through effects on reproduction, mortality, and movement (Andrewartha and Birch 1954, White 1978, 1993). When food scarcity is seasonal and predictable, insects cope by engaging in diapause-mediated responses such as dormancy or seasonal migration (Tauber and Tauber 1993). Incidences of food depletion within a season tend to be unpredictable both on a spatial and temporal scale and may be of short duration relative to the life cycle of an insect. Several studies have indicated that within-season food scarcity is a chronic phenomenon for the carnivore trophic level and that, in addition to having consequences on demographic parameters, it also impacts biotic interactions such as inter- and intraspecific competition, cannibalism, and intraguild predation (Lenski 1984, Wise 1993, 2006; Bilde and Toft 1998). Although aphid-

dophagous lady beetles consume a wide range of food, aphids are considered their preferred and essential prey because they ensure complete and fast preimaginal development, low mortality, larger body size, and higher fecundity (Hodek and Honěk 1996). Preference for aphids by lady beetles makes them particularly susceptible to nutritional stress caused by within-season food scarcity because aphid populations are both spatially and temporally ephemeral (i.e., exhibit “boom-and-bust” dynamics over short intervals) in nature (Dixon 1985, 2000).

Aphid populations are typically distributed in space as patches (i.e., discrete spatial units of the environment within which resources are aggregated) (Hassell and Southwood 1978). The patchy distribution of aphids is often a consequence of habitat heterogeneity and aphid existence in transient colonies (i.e., aggregations of nymphs around their mothers) on plant tissues (Dixon 1985, 2000). The abundance of aphids in a colony or a patch is mainly influenced by three factors: abundance of natural enemies, quality of host plants, and weather conditions. Predators reduce aphid densities directly by consuming individual aphids as well as indirectly by their presence, which elicits predator avoidance responses in aphids. Predator avoidance responses include leaving the feeding site, dislodging from host plants (in response to alarm pheromones), and trans-generational production of

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winged morphs (offspring) (Dixon 1985, McConnell and Kring 1990, Losey and Denno 1998, Dixon and Agarwala 1999, Weisser et al. 1999, Mondor et al. 2005, Nelson and Rosenheim 2006). The combined effect of these factors is the creation of highly variable and unpredictable food resources for aphid predators like lady beetles (Kindlmann and Dixon 1999, Dixon 2000).

Strategies adopted by insects when confronted by a sudden unpredictable environmental change, such as food depletion, include staying in place until the condition ends, leaving the affected area, or staying for a while and leaving if no improvement occurs (Taubert et al. 1986). Although these strategies work well for adult lady beetles, their effectiveness in larvae may be limited. For example, larvae of lady beetles have limited dispersive abilities and are therefore more vulnerable to food depletion than adults, which can avoid nutritional stress by readily leaving patches with limited food resources. Another behavior that seems to allow lady beetles to survive within-season food scarcity is the ability to assess the quality of prey patches by females. This behavior is shown by a tendency to lay eggs in the vicinity of aggregations of aphids that are likely to sustain larval development (Dixon 2000). Even if this is an inherent strategy of lady beetles, we hypothesize that it does not always ensure adequate prey supply to developing larvae because other factors, including weather, regularly cause a decline or disappearance of aphids before larvae complete their development. Evidence in support of our hypothesis is the smaller body size of field-collected adults relative to that of laboratory-reared adults fed *ad libitum* aphids (Obrycki et al. 1998, M.W.P., unpublished data).

This study examined the ability of lady beetle larvae to cope with unpredictable food resources. We postulate that adaptations that underlie such a coping ability are critical to the success of a lady beetle species in the field. We chose the fourth (final) instar as the developmental stage to subject to food scarcity for several reasons. First, it is critical to the fitness of an individual insect because the size attained by fourth instars determines adult size, which in turn is related to other life history traits including fecundity, longevity, and mating success in males (Hodek and Honěk 1996, Dixon 2000). Second, food scarcity should affect fourth instars more than the younger (first-third) instars because the terminal developmental position of fourth instars makes them more vulnerable to the "bust" part of the "boom-and-bust" aphid population dynamics (Dixon 2000). Third, the high consumption of aphids by fourth instars (60–80% of aphids consumed during larval stage) is likely to subject them to localized prey depletion (Hodek and Honěk 1996). We used three of the most common species of aphidophagous lady beetles in agroecosystems throughout the Great Plains of the United States: *Coleomegilla maculata* (DeGeer), *Hippodamia convergens* Guerin-Meneville, and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae).

Our goal was to specifically quantify how the three species respond to starvation periods simulating the boom-and-bust dynamics of aphid populations in terms of (1) survival to adult stage, (2) length of survival period (i.e., starvation resistance), (3) weight loss, (4) duration of fourth stadium, (5) body weight of fourth instars at pupation, (6) duration of pupal stadium, and (7) adult size. The approach used here differs from that used in studies simulating effect of suboptimal food where reduced quantities of food are offered on a daily basis to insects (Giles et al. 2001, 2002; Phoofolo et al. 2007). We believe that our approach created an acute nutritional stress, whereas offering reduced daily food quantities chronically stresses lady beetle larvae.

Materials and Methods

Source of Aphids and Lady Beetles. The source of food provided to lady beetle larvae was the greenbug, *Schizaphis graminum* (Rondani) (Homoptera: Aphididae), an aphid species that is often an important food source for lady beetles in cereal farmlands in the Great Plains. Greenbug colonies were maintained on sorghum (*Sorghum bicolor* L. Moench; variety SG-822) plants in a greenhouse ($22 \pm 3^\circ\text{C}$) under natural light supplemented by electrical light in the evening to provide a 16:8 (L:D)-h photoperiod. Sorghum was grown in 15-cm-diameter pots covered with plexiglass or acetate cylinders (33 cm tall) that were vented with nylon mesh fabric on the top end and in two locations on the side to provide air flow while keeping plants free from aphid infestation. When plants were ≈ 33 cm tall, cylinders were removed, plants were placed inside cages (constructed by covering 50 by 50 by 50-cm wooden frames with nylon mesh fabric), and infested with greenbugs. Aphids were collected daily from heavily infested plants as needed for the feeding experiment. Plants showing signs of severe greenbug injury (significant necrosis) were replaced with fresh, greenbug-infested plants as needed.

In April and May 2004, we collected adult lady beetles of all three species from northcentral Oklahoma alfalfa and wheat fields. Ten mating pairs of each species were individually maintained in half-pint (0.24 liter) paper cartons (Neptune Paper Products, Jersey City, NJ) covered with fine mesh in table-top environmental chambers (22°C , 16:8 [L:D]-h photoperiod). Pairs were provided daily with an unlimited supply of greenbugs, moist cotton, and a supplementary 1:1 mixture of honey and wheat (Prod 176; Planet Natural, Bozeman, MT) to stimulate egg production. Egg masses from each mating pair were collected daily and reared separately in 10-ml glass vials stopped with cotton. On hatching, larvae were transferred to rearing containers and provided with greenbugs *ad libitum* until they molted into third instars.

Food Deprivation Experiments. All experiments were carried out in a table-top environmental chamber at 22°C and a photoperiod of 16:8 (L:D) h. Within 24 h of becoming third instars, larvae were placed individually in vials stopped with cotton and were

supplied with ad libitum greenbugs until molting to fourth instars. Fourth instars of each lady beetle species were randomly assigned to one of six food deprivation treatments: (1) larvae fed for the first 5 d (0-d food deprivation period), (2) larvae fed only for the first 4 d (1-d food deprivation period), (3) larvae fed only for the first 3 d (2-d food deprivation period), (4) larvae fed only for the first 2 d of the fourth stadium (3-d food deprivation period), (5) larvae fed only for the first day of the fourth stadium (4-d food deprivation period), and (6) individuals starved throughout the fourth stadium (5-d food deprivation period). Feeding larvae for the first 5 d of the stadium was equivalent to feeding until initiation of pupation because, in this treatment, fourth instars of all three species ceased feeding and entered the prepupal stage. The number of larvae assigned to each treatment ranged from 12 to 21 for each lady beetle species.

The effect of food deprivation period on development time of fourth instars and pupae was determined by daily examination of larvae and pupae for survival and length of stadia. To measure effects of food deprivation period on weight at pupation and adult eclosion, we determined weight (by a digital Satorium M3P microbalance, resolution: 0.001 mg) of larvae within 24 h of pupation and that of adults within 24 h of eclosion. The gender of larvae that successfully developed to adulthood was also determined.

Voucher Specimens. Voucher specimens of *C. maculata*, *H. axyridis*, and *H. convergens* adults were deposited in the Department of Entomology and Plant Pathology Museum at Oklahoma State University, Stillwater, OK.

Statistical Analyses. All analyses were performed using SAS version 8.2 for Windows (SAS Institute 1999). The Fisher exact test (PROC FREQ) was used to examine the effects of food deprivation period on both survival to adult stage and sex ratios of the larvae that successfully developed to adults (maturation). Where the Fisher exact test resulted in $P < 0.05$, a post hoc Tukey-type multiple comparison procedure for proportions was used to identify significant differences between pairs of treatments (Zar 1999).

The effects of food deprivation period and gender on development time and body weight were assessed by fitting linear mixed models separately for development time of fourth instars and pupae and for weight of fourth instars within 24 h of pupation and adult weight on eclosion. Food deprivation period, gender, and their interaction were included in the models as fixed effects. Mating pairs used as sources of larvae were incorporated in the models as random effects. We took a mating pair as a surrogate for genotype and included it as a class variable in these analyses to account for effects of innate (genetic) variation and correlation among our sampling units (i.e., individual fourth instars of *C. maculata*, *H. convergens*, and *H. axyridis*). Analysis computations were performed by PROC MIXED using the restricted maximum-likelihood estimation method. Effects of food deprivation period were further evaluated using orthogonal polynomial contrasts to determine linear and nonlinear

Table 1. Percent of the fourth instars of *H. convergens*, *C. maculata*, and *H. axyridis* surviving to adult stage according to the number of days without food

Food deprivation period (d) ^a	<i>C. maculata</i>		<i>H. axyridis</i>		<i>H. convergens</i>	
	<i>n</i>	Percent survival	<i>n</i>	Percent survival	<i>n</i>	Percent survival
0	20	100Aa	16	93.8Aa	12	83.3Aa
1	20	95.0Aa	17	94.1Aa	13	92.3Aa
2	20	100Aa	17	94.1Aa	14	85.7Aa
3	21	52.4Ab	15	66.7Aa	14	92.9Ba
4	21	14.3Ac	17	5.9Ab	14	35.7Ab
5	21	0c	16	0b	14	0c

^a Number of consecutive days of the fourth stadium during which lady beetle larvae were deprived of food until they either pupated or died. See text for details. Percentages followed by the same lowercase letter in the same column and by the same uppercase letter in the same row are not significantly different at $P = 0.05$.

trends in response variables. If polynomial contrasts were significant, analysis of covariance (ANCOVA; PROC MIXED), with gender as the main effect, food deprivation period as the covariate, and mating pair as a random effect, was used to quantify the relationship between dependent variables and food deprivation period. The test for normality of data (PROC UNIVARIATE) performed before analyses by PROC MIXED indicated that no transformations were needed for any data.

Results

Survival and Sex Ratios. None of the larvae that were denied food throughout the fourth stadium survived to pupation (Table 1). Among the remaining treatments, the percentage of fourth instars of each species surviving to the adult stage was influenced by food deprivation period (Fisher exact test; $P < 0.0001$). The highest survival levels for each lady beetle species were found in the groups for which food deprivation period was ≤ 2 d of the fourth stadium (Table 1). Survival among the lady beetle species differed for larvae deprived of food for 3 d of the stadium; significantly more *H. convergens* larvae survived to pupation compared with the other two species (Table 1).

The sex ratio of *C. maculata* and *H. convergens* fourth instars that developed to adult stage was not influenced by food deprivation period (Fisher exact test; $P = 0.36$ and $P = 0.78$, respectively). The sex ratio differed significantly among treatments for *H. axyridis* ($P = 0.018$); there were fewer females surviving to adulthood when larvae were deprived of food for 3 d of the stadium than when larvae were deprived of food for 2, 1, or 0 d of the stadium (Table 2). Only one *H. axyridis* (a male) survived to adulthood in the group deprived of food for 4 d of the stadium (Table 2).

Survival Time of Larvae Subjected to Different Periods of Starvation. Because all individuals starved throughout the stadium (5-d food deprivation period) as well as the majority of those deprived of food for 4 d of the stadium died before pupating, we used an analysis of variance (ANOVA) to determine whether sur-

Table 2. Percent of the fourth instars of *H. convergens*, *C. maculata*, and *H. axyridis* developing into adult females according to the number of days without food

Food deprivation period (d) ^a	<i>C. maculata</i>		<i>H. axyridis</i>		<i>H. convergens</i>	
	n	Percent female	n	Percent female	n	Percent female
0	20	50.0	15	71.4	10	50.0
1	19	42.1	16	50.0	12	50.0
2	20	55.0	16	62.5	12	50.0
3	11	18.2	10	10.0	13	30.8
4	3	33.3	1	0	5	60.0
P value		0.36		0.018		0.78

^a Number of consecutive days of the fourth stadium during which lady beetle larvae were deprived of food until they either pupated or died. See text for details.

vival time was influenced by either of these treatments or lady beetle species. We did not include other treatments because fewer than three fourths of instars died before pupating when food deprivation lasted >2 d, and statistical comparison involving these treatments was not possible. Fourth instars deprived of food for 4 d of the stadium survived much longer than those that were deprived of food for 5 d as fourth instars ($F = 62.38$; $df = 1,77$; $P < 0.0001$; Fig. 1). The effect of species on survival time was statistically significant ($F = 4.08$; $df = 2,77$; $P = 0.02$), but because the interaction effect between treatment (food deprivation period) and species was also significant ($F = 5.87$; $df = 2,77$; $P = 0.004$), species means were compared separately for each food deprivation period using the SLICE option of the LSMEANS statement in the SAS MIXED procedure. Species differences in the survival time caused by starvation were significant among larvae deprived of food for 4 d of the stadium: *H. convergens* > *H. axyridis* > *C. maculata* ($F = 8.21$; $df = 2,77$; $P = 0.0006$), but not among larvae deprived of food for 5 d as fourth instars ($F = 0.07$; $df = 2,77$; $P = 0.94$; Fig. 1).

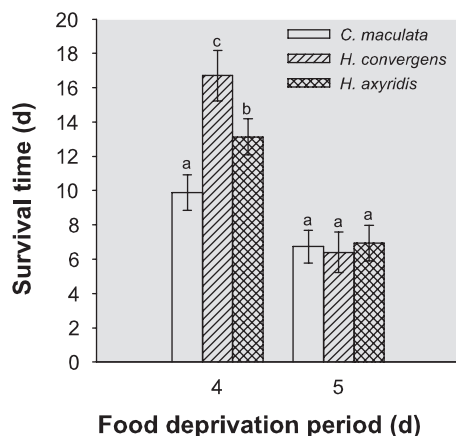


Fig. 1. Mean (\pm SE) time to death by starvation (starvation resistance) of fourth instars versus food deprivation period. For each food deprivation period, means followed by the same letter are not significantly different.

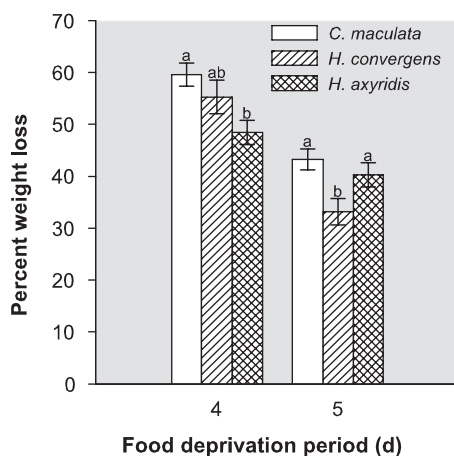


Fig. 2. Percentage of weight lost at death of beetle larvae deprived of food for 4 and 5 d of the fourth stadium. For each food deprivation period, means followed by the same letter are not significantly different.

Loss of Body Weight During Starvation. We used ANOVA to test the effects of food deprivation period and lady beetle species on the percentage of body weight lost during starvation for larvae that died when starved throughout the stadium (i.e., 5-d food deprivation period) and when deprived of food for 4 d of the stadium. The percentage of initial body weight lost was affected by food deprivation period ($F = 59.24$; $df = 1,77$; $P < 0.0001$) and lady beetle species ($F = 6.47$; $df = 2,77$; $P = 0.0025$). When deprived of food for 4 d of the stadium, *C. maculata* lost a higher percentage of initial body weight than *H. axyridis*. Percentage weight loss of *H. convergens* did not differ from that of *C. maculata* or *H. axyridis* (Fig. 2). Neither *C. maculata* nor *H. axyridis* fourth instars differed in the percentage of initial body weight lost when starved throughout the stadium; both lost a significantly higher percentage of their initial body weight than *H. convergens* (Fig. 2).

Body Weight. The weight of fourth instars within 24 h of pupation was highly correlated to adult body weight in each species (*C. maculata* Pearson's correlation coefficient, $r_s = 0.960$; $P < 0.0001$; $n = 73$, *H. convergens*, $r_s = 0.984$; $P < 0.0001$; $n = 52$, and *H. axyridis*, $r_s = 0.989$; $P < 0.0001$; $n = 56$). Therefore, only data on weight of fourth instars are presented. Gender differences in body weight were significant in both *C. maculata* and *H. convergens* (Table 3; Fig. 3). The effect of food deprivation period on body weight decreased linearly in all species ($P < 0.0001$), with a significant quadratic trend ($P < 0.05$) for both *C. maculata* and *H. axyridis*, indicating an accelerating decline in body weight with an increase in food deprivation period (Table 3; Fig. 3). The maximum predicted weight for *C. maculata* is 17.201 and 15.201 mg for females and males, respectively, and for *H. axyridis* is 39.794 and 38.024 mg, respectively. Although the quadratic effect was not statistically significant in *H. convergens*, it was included in describing the relation-

Table 3. Results of ANOVA (SAS mixed procedure) to evaluate effects of food deprivation period on fourth-instar body weight, duration of fourth stadium, and duration of pupal stadium for *C. maculata*, *H. convergens*, and *H. axyridis*

Response variable	Source of variation	<i>C. maculata</i>			<i>H. convergens</i>			<i>H. axyridis</i>		
		df ^a	F-value	P	df ^a	F-value	P	df ^a	F-value	P
Fourth-instar body weight	Treatment	4, 59	16.31	<0.0001	4, 39	17.81	<0.0001	3, 43	32.61	<0.0001
	Linear	1, 59	51.50	<0.0001	1, 39	61.79	<0.0001	1, 43	88.77	<0.0001
	Quadratic	1, 59	3.32	0.04	1, 39	3.04	0.09	1, 43	6.10	0.03
	Cubic	1, 59	0.72	0.41	1, 39	0.15	0.70	1, 43	0.72	0.53
	Quartic	1, 59	1.66	0.20	1, 39	1.64	0.21			
	Gender	1, 59	10.16	0.002	1, 39	15.67	0.0003	1, 43	0.20	0.65
	Treatment \times gender	4, 59	0.35	0.84	4, 39	0.23	0.92	3, 43	0.68	0.57
Duration of fourth stadium	Treatment	4, 59	1.32	0.27	4, 39	0.47	0.75	3, 43	4.56	0.007
	Linear							1, 43	12.84	0.0009
	Quadratic							1, 43	4.88	0.0325
	Cubic							1, 43	0.44	0.5099
	Gender	1, 59	0.00	0.96	1, 39	0.76	0.39	1, 43	0.21	0.65
Duration of pupal stadium	Treatment \times gender	4, 59	1.83	0.13	4, 39	1.13	0.35	3, 43	0.78	0.51
	Treatment	4, 59	1.02	0.40	4, 39	0.08	0.99	3, 43	2.17	0.10
	Gender	1, 59	0.02	0.90	1, 39	0.03	0.85	1, 43	0.20	0.66
	Treatment \times gender	4, 59	0.12	0.97	4, 39	0.08	0.99	3, 43	0.22	0.88

^a ANOVA performed for individuals that survived to the adult stage.

ship between food deprivation period and body weight because the change in weight also showed an accelerating decline in this species (Fig. 3). The maximum predicted weight for *H. convergens* is 26.695 and 23.002 mg for females and males, respectively. ANCOVA showed no significant interaction between gender and food deprivation period, indicating a similar relationship between body weight and food deprivation period for both males and females of all three species ($F = 0.00$; $df = 1, 64$; $P = 0.954$ for *C. maculata*, $F = 0.08$; $df = 1, 44$; $P = 0.775$ for *H. convergens*, $F = 0.81$; $df = 1, 46$; $P = 0.374$ for *H. axyridis*).

Length of Fourth and Pupal Stadia. The length of fourth stadium in *C. maculata* and *H. convergens* remained constant and was not dependent on either food deprivation period or gender (Table 3; Fig. 4). Lack of significant effects in both species remained even after pooling the data over gender (*C. maculata*: $F = 1.53$; $df = 4, 64$; $P = 0.20$; *H. convergens*: $F = 0.78$; $df = 4, 44$; $P = 0.54$). The length of fourth stadium in *H. axyridis* increased significantly with food deprivation period. This increase was curvilinear for both sexes as indicated by polynomial contrasts and ANCOVA (Table 3; Fig. 4).

The length of the pupal stadium was not influenced by food deprivation period or gender in any of the species (Table 3). Additionally, there were no significant effects of food deprivation period even after data were pooled across gender (*C. maculata*: $F = 1.42$; $df = 4, 64$; $P = 0.24$; *H. convergens*: $F = 0.13$; $df = 4, 44$; $P = 0.97$; *H. axyridis*: $F = 2.41$; $df = 3, 47$; $P = 0.08$). The length of the pupal stadium ranged from (mean \pm SE) 5.31 ± 0.64 to 6.19 ± 0.36 d in *C. maculata*, 7.06 ± 0.40 to 7.25 ± 0.42 d in *H. convergens*, and 8.41 ± 0.32 to 8.69 ± 0.30 d in *H. axyridis*.

Discussion

Results from this study suggest that successful development to pupation and adulthood by fourth instars is dependent on prey availability during the early

part of the fourth stadium in each of the three lady beetle species. Access to adequate aphid prey during the first 3 d of the fourth stadium seems to be critical, because fourth instars deprived of food after day 3 of the stadium showed no difference in survival levels, regardless of species. In contrast, all larvae deprived of aphids throughout the stadium died before pupation. The ability to survive and successfully complete development when deprived of food is an indication of an important adaptive strategy that should allow lady beetles to cope with the highly unpredictable and variable food resources in nature (i.e., the boom-and-bust dynamics of aphid populations over short intervals).

The length of time to death by starvation can be taken as a measure of starvation resistance. Starvation resistance involves a complex of physiological adjustments that enable organisms to survive and reproduce under nutritional stress (Hoffmann and Parsons 1991). Physiological adjustments resulting in increased length of time to death by starvation translate into an increased probability of encounters with food and recovery from starvation. Results reported here indicate that feeding on the first day of the fourth stadium significantly increases the length of time to death by starvation in all three species (Fig. 1). Comparison of the length of time to death by starvation among species shows no differences among fourth instars that had no access to food (i.e., 5-d food deprivation period), whereas those that fed only on day 1 of the fourth stadium (i.e., 4-d food deprivation period) showed significant differences in survival time among species: *H. convergens* > *H. axyridis* > *C. maculata* (Fig. 1). This is contrary to the size-dependent resistance to starvation hypothesis that is based on two allometric relationships, (1) metabolic rates scale as $W^{0.75}$ and (2) energy stores scale as $W^{1.0}$, where W is body weight (Peters 1983, Cushman et al. 1993). Because energy reserves increase with body size at a faster rate than metabolic rates, this hypothesis predicts that larger organisms/species should resist star-

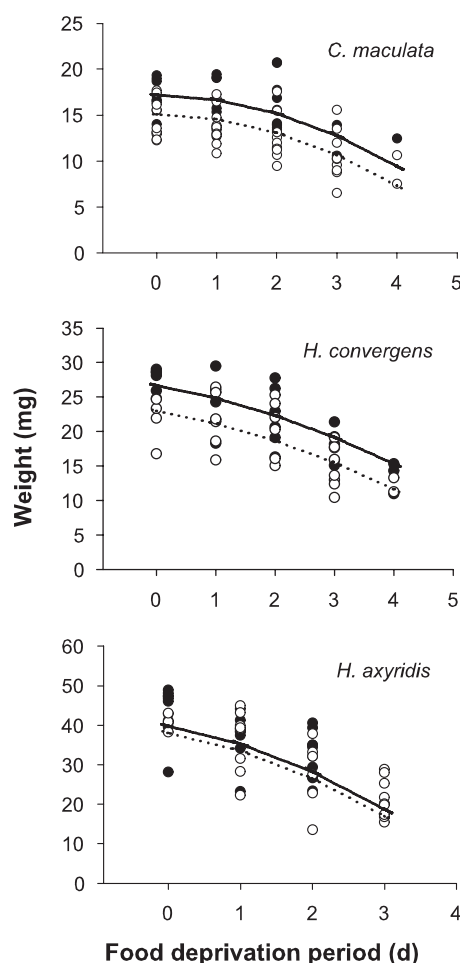


Fig. 3. Relationship between food deprivation period and body weight of fourth instars ≤ 24 h before pupation. The relationship was described by the following equations: *C. maculata*, $W = 15.094 \pm 0.901 + 2.117 \pm 0.447X - 0.0918 \pm 0.524D - 0.464 \pm 0.154D^2$; *H. convergens*, $W = 22.991 \pm 1.552 + 3.693 \pm 0.798X - 1.515 \pm 1.002D - 0.332 \pm 0.258D^2$; *H. axyridis*, $W = 38.017 \pm 3.368 + 1.770 \pm 1.278X - 3.319 \pm 1.744D - 1.235 \pm 0.585D^2$; where W is body weight (mg), D is food deprivation period (d), and $X = 1$ if gender was female (●; solid line) and 0 if male (○; dotted line).

vation longer. Body weight for the three lady beetle species ranks as *H. axyridis* > *H. convergens* > *C. maculata* during both larval and adult stages (Fig. 3).

An ability to reduce metabolic rate during food shortages has been shown to be a mechanism for starvation resistance (even after correcting for size) in *Drosophila* spp. (Oudman et al. 1994, Djawdan et al. 1997), although there are studies that contradict this finding (Service 1987, Harshman et al. 1999). Assuming that weight lost during starvation is proportional to metabolic rate (Baumgaertner et al. 1981), it seems that percent weight loss of larvae in this study (Fig. 2) is not related to metabolic rate in these beetles, because there is a poor correlation between percent weight loss and length of time to death by starvation.

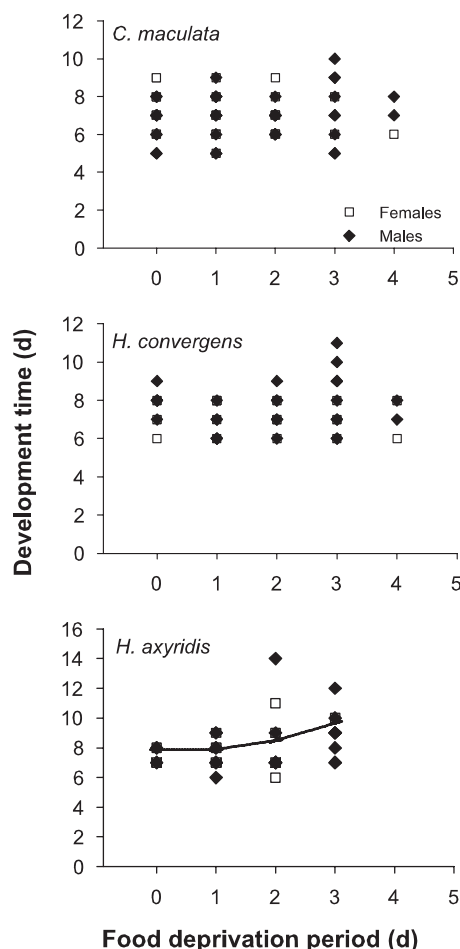


Fig. 4. Relationship between food deprivation period and development time of fourth instars. Development time did not vary significantly with food deprivation period for *C. maculata* or *H. convergens* (no line shown). Development time for *H. axyridis* increased significantly with food deprivation period according to the following equation: $SL = 7.863 \pm 0.588 - 0.259 \pm 0.463D + 0.286 \pm 0.153D^2$, where SL is stadium length (d) and D is food deprivation period (d).

Both body weight of fourth instars within 24 h of pupation and adult body weight responded in a similar fashion to the different food deprivation periods; body weight declined in an accelerating pattern with an increase in food deprivation period (Fig. 3). Although our study tested the effects of acute nutritional stress on fourth instars, the results on body weight showed a pattern similar to the one obtained under chronic nutritional stress, where food offered to larvae ranged from suboptimal to surplus amounts (on a daily basis) (Hodek and Honěk 1996, Dixon 2000, Giles et al. 2001, 2002). In contrast, length of the fourth stadium in this study responded differently from studies evaluating chronic nutritional stress. Length of the fourth stadium of *H. convergens* and *C. maculata* larvae was not significantly influenced by food deprivation period; however, length of the fourth stadium of *H. axyridis*

larvae deprived of food for 3 d of the fourth stadium required 2 d longer than those that were fed everyday (Table 3; Fig. 4). In studies testing the effects of chronic nutritional stress, rate of development (i.e., inverse of length of stadium) increased as food quantity increased up to satiation, beyond which it leveled off (Hodek and Honěk 1996, Dixon 2000, Giles et al. 2001, 2002).

The difference in responses of fourth instars to chronic versus acute nutritional stress can be explained in terms of a model developed by Gutierrez et al. (1981) and refined by Baumgaertner et al. (1987), to relate food intake, assimilation, and energy allocation between growth, development, and metabolic demands in immature lady beetles. According to this model, energy will be allocated to growth (and reserve accumulation) only when consumed food exceeds energy requirements for maintenance (metabolic costs); otherwise, under starvation, the larva loses weight as energy from reserves and other tissues is used for survival (Hodek and Honěk 1996). Therefore, under chronic nutritional stress, fourth instars take a longer time to grow to the threshold size necessary for metamorphosis to occur because more energy is diverted toward maintenance rather than somatic growth. Our results indicate that when larvae experienced acute nutritional stress after feeding ad libitum for the first 2 d of the fourth stadium, they did not pupate immediately, even though they may have attained a threshold weight necessary for metamorphosis. If the delay in pupation also occurs in the field, it is likely to increase the larval chances of encountering and consuming more prey, leading to larger adults. However, delayed pupation may result in potential risks of mortality from natural enemies and/or loss of critical weight. However, our results indicate that fourth instars that had access to prey even after attaining the threshold size continued to feed and grew bigger. This continued feeding enables individuals to increase their fitness by producing more offspring as adults.

Variation in resource abundance and quality is considered to be very important for determining competitive outcomes among species that belong to the same trophic guild (Hoffmann and Parsons 1991). Based on the findings from this laboratory study, it would seem that *H. convergens* is better able to cope with acute nutritional stress than either *C. maculata* or *H. axyridis*. Although the results from this study cannot answer the question of how well this ability to cope with nutritional stress translates into surviving in the wild, it does offer a possible explanation of the relative abundances of the three lady beetle species in Oklahoma (and the U.S. southern plains), where *H. convergens* is the most abundant species (Elliott and Michels 1997, Lee et al. 2005, M.W.P., unpublished data).

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